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Spatio-temporal Analysis of Cortical Activity Evoked by Gustatory Stimulation in Humans

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Abstract

Gustatory activated regions in the cerebral cortex have not been identified precisely in humans. In this study we recorded the magnetic fields from the brain in response to two tastants, 1 M NaCl and 3 mM saccharin. We estimated the location of areas activated sequentially after the onset of stimulation with magnetic source imaging. We investigated the primary gustatory area (area G) precisely, and found it at the transition between the parietal operculum and the insular cortex. The central sulcus was activated less frequently than area G but with almost the same latency in cases of NaCl stimulation. Following area G, we found activation in several cortical regions, e.g. both the frontal operculum and the anterior part of the insula, the hippocampus, the parahippocampal gyrus and the superior temporal sulcus.

Introduction

The gustatory-related regions of the cerebral cortex in human beings have been the subject of argument for a long time (since Penfield and Boldrey, 1937). Although intensive electrophysiological experiments on gustatory areas have been made on subhuman primates (for reviews see Ogawa, 1994; Rolls, 1989), research on human beings has been limited to clinical observation of patients with brain damage (e.g. Motta, 1959). In most cases, damage is not confined toa pinpoint place in the brain but instead involves a wide area, which makes clinical study difficult. Thus little has been discovered about the location and function of gustatory cortex in the human brain to date.

Recent development of imaging techniques has yielded various non-invasive methods, e.g. functional magnetic resonance imaging (fMRI), positron emission tomography (PET) and magnetoencephalography (MEG), and allows us to measure the cerebral activities of living human subjects without surgical invasion. Among these methods, PET and fMRI have insufficient temporal resolution to trace the cortical flow of taste information. Kinomura *et al.* (1994) revealed many gustatory-related regions in human cerebral cortex with PET. MEG, on the other hand, has good temporal resolution, and can give a good estimation of thelocation of the activity much more precisely than electroencephalography (EEG), because the magnetic field generated from living brain is free from distortion by the skull. However, a pulse-like presentation of a pure tastant free from tactile stimulation is indispensable in the measurement of gustatory-related cerebral activities by MEG or EEG. Because of the difficulty in building such a stimulator, only a few reports have been made of gustatory evoked potentials (Funakoshi and Kawamura, 1971; Kobal, 1985; Prescott, 1989; Plattig, 1991) in a long history of EEG measurement.

We devised a tactile-free taste delivery system with a rise time of 20 ms or less (Kobayakawa *et al.*, 1996a). By integrating both the taste stimulator and a 64-channel whole-head SQUID MEG measurement system, we measured the magnetic fields evoked by gustatory stimulation inshort latencies (e.g. <200 ms for NaCl and <400 ms forsaccharin), and located the source of the first peak, i.e.the primary gustatory area (area G), at the transition between the operculum and insular cortex (Kobayakawa *etal.*, 1996b). However, we could not determine the precise location; that is, it is not clear whether the area is at the transition between the frontal operculum and insula, as in macaque monkeys (Ogawa *et al.*, 1985), or between the parietal operculum and insula. On the other hand, it is

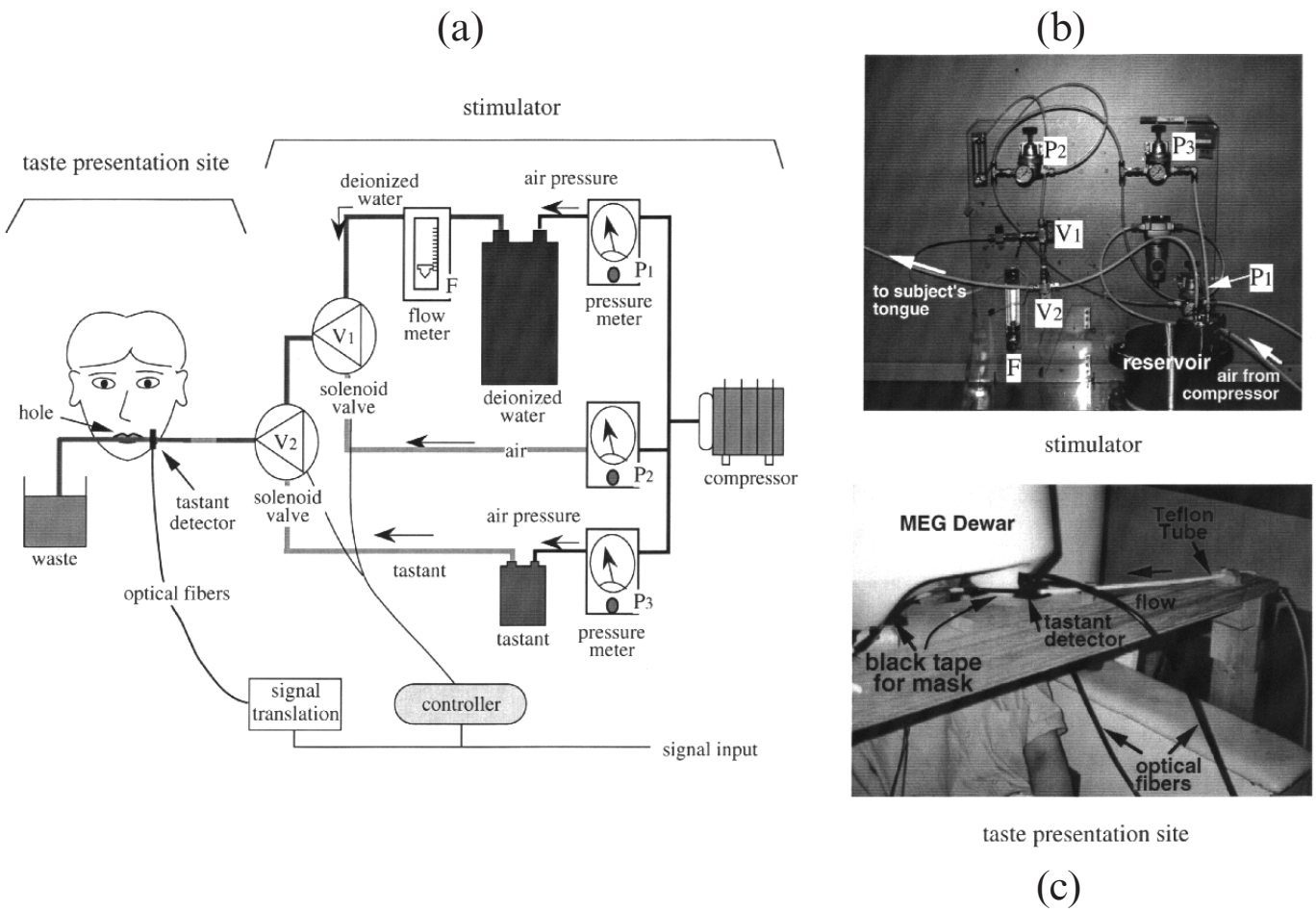

Figure 1 The schematic drawing **(a)** and actual photograph **(b)** of the taste stimulation device, taste presentation site, subject and MEG equipment while being stimulated **(c)**. The water, tastants and air flow in the tube were switched by solenoid valves which were controlled by a personal computer. Stimuli were presented to the tongue through a hole opened in the wall of a Teflon tube. The subject took the tube in his/her mouth, then covered the hole with the tip of his/her tongue. Liquid and air then flowed over the part of the tongue that covered the hole. We used an optical sensor to measure the time at which the tastants reached the tongue, in order to obtain a trigger for averaging the GEMs. The tastants were colored red, whereas air and water were uncolored. Black tape covered the Teflon tube close to mouth to prevent subjects from seeing the change of color in the tube.

known that the oral representation region in the primary somatosensory area (SI) is activated as fast as area G in monkeys when peripheral taste nerves are stimulated electrically (Ogawa *et al.*, 1985), though only area G has previously been found to contribute to the gustatory evoked magnetic fields (GEMs). Further, we noticed a lack of the previously defined first peak of GEMs in a few cases with an increased number of subjects and recording sessions.

In the present study, therefore, the aim of the investigation was threefold. We attempted (i) to clarify the contribution of SI to the first peak of GEMs by increasing the number of subjects and sessions to see if the afferent projection to SI from the thalamic gustatory area is the same in humans as inmonkeys (Ogawa *et al.*, 1985); (ii) to determine whether area G was anterior to the central sulcus or posterior to it;and (iii) to examine the sequence of activation of the gustatory-related cortical regions revealed by PET after area G to trace the possible flow of taste information.

Materials and methods

Subjects

Seven neurologically healthy volunteers (four males and three females, age 21–37 years) participated in the experiments. They were informed about the nature of the experiment, and agreed to become subjects. The study was conducted inaccordance with the revised version of the Helsinki declaration and was approved by the National Institute of Bioscience and Human-Technology, Japan.

Stimulation

The taste delivery system has previously been described in detail (Kobayakawa *et al.*, 1996a), and is represented in Figure 1a. In short, deionized water and tastants were driven through the system by compressed air. The small amount of air that separated the tastant and water was released into the tube for as short a duration as possible

(90ms) to minimize the chance of the subject feeling a pressure difference between the liquid and air. The water, tastants and air flows in the tube were switched by solenoid valves which were controlled by a personal computer (Figure 1a,b). Stimuli were presented to the tongue through a hole (3 × 9 mm) opened in the wall of a Teflon tube. The subject took the tube in his/her mouth, then covered the hole with the tip of his/her tongue. Liquid and air then flowed over the part of the tongue that covered the hole (Figure 1c). Since the flow of the liquid and air generated a slight negative pressure, the tip of the tongue was sucked slightly into the hole, hence air and the liquid did not leak outside the tube. We used an optical sensor to measure the time at which the tastants reaches the tongue, in order to obtain a trigger for averaging the GEMs. The tastants were colored red, whereas air and water were uncolored. Black tape covered the Teflon tube close to mouth, to prevent subjects from seeing changes in the color in the tube (Figure 1c).A light outside the shielded room was passed through the Teflon tube just before the hole and the tastant was detected by a photo-transistor. The voltage generated by thephoto-transistor was converted into a digital signal by an A/D converter. The distance between the measurement location and the hole on the tube was 6.5 cm. It took ~300 ± 2.9 ms (mean ± SD) for the fluid to run that distance. The rise-time to 80% of the signal was 16.5 ± 1.49 ms.

Solutions of 1 M NaCl and of 3 mM saccharin were used as tastants. The fluid was presented at the central, front edgeof the subject's tongue, the part known to have high sensitivity to these tastes. The stimulus duration was 400 ms and the inter-stimulus interval 30 s. The tastant and water were kept at 36°C, approximately the same temperature as that of the tongue. The flow rate of the water and stimuli was 200 ml/min. During the recording session, the subjects wore earplugs. They were instructed not to change their head positions, keep their eyes open and watch a fixation point in front of them. Before each recording, we accustomed each subject to this experimental condition. After each recording, subjects were asked about the quality of thetaste. The averaged intensity was 2.85 for salty stimuli and 2.55 for sweet in seven subjects, and there was no significant difference. They were also asked about the somatic (i.e.tactile and thermal) sensation incidental to the taste stimulation; however, none of them reported any, which is consistent with the previous finding that there was no MEG response to water stimuli (Kobayakawa *et al.*, 1996b).

We presented only one tastant to a given subject in each session. Each subject participated in one session per day, in order to avoid fatigue. The sessions for a given subject were separated by >2 days.

Recordings of magnetic fields

For measurement of magnetic fields, we used a 64-channel whole-head SQUID system (CTF Systems Inc., Canada; Figure 1b). The sampling rate for the MEG signal was 250 Hz and the low-pass filter was set at 40 Hz. Forty trials were presented to each subject per session. After the experiment, the signals from the optical sensor were used as a trigger for off-line averaging of the data. Trials contaminated by eye movement were rejected. The number of trials used for averaging was nearly 35. If the number of available trials was <30, the session was rejected. The number of sessions available for data processing was 23 (11 for NaCl and 12 for saccharin).

Three-dimensional MRI scans were obtained for all subjects (SIEMENS: 1.5 tesla for six subjects, 1.0 tesla forone subject). For source modeling, MRI head shape datawere used to determine the fitting sphere for each subject's head. Estimation of equivalent dipoles (ECDs) were carried out to minimize the estimation error, based onthe Grynszpan–Geselowitz equation (Grynszpan and Geselowitz, 1973; see Kobayakawa *et al.*, 1996b). The error E was calculated using the following formula:

$$E = \frac{\sum_{n=1}^{64} \left(\hat{X}_n - X_n \right)^2}{\sum_{n=1}^{64} X_n^2}$$

where X_n is the magnitude of the neuromagnetic field at the nth sensor and $\hat{X}_n$ is the calculated magnitude at the same sensor based on the theoretical model. The goodness of fit was calculated as $1 - E$. The locations as well as the strength of the ECDs in each subject were estimated from magnetic fields obtained from 64 sensors.

The location of the head with respect to the sensors was determined by measuring the magnetic fields produced by small currents delivered to three coils attached to the scalp, located at the nasion and the two preauricular points. When we obtained the subjects' MR image, oil-filled pellets were attached to the same landmarks as used in the MEG experiment. The positional information for the centers of three white balls in the subject's MR image, i.e. the images ofthe oily pellets, were used to align the MEG data with theparticipant's MR image. The coordinates of the dipole centers of gravity were overlaid on individual MRI slices toshow the corresponding locations in the brain, after alignment.

Results

Gustatory evoked magnetic fields

Figure 2 shows superimposed magnetic fields of 12 out of the 64 channels, and an isocontour map over the head, inresponse to two tastants. These 12 channels had remarkable changes in magnetic fields, at 370 ms after the onset ofsaccharin presentation and at 110 ms after NaCl. Both isocontour maps showed that the induced magnetic field was directed from the front to the back on the left side of the head and from the back to the front on the right side.

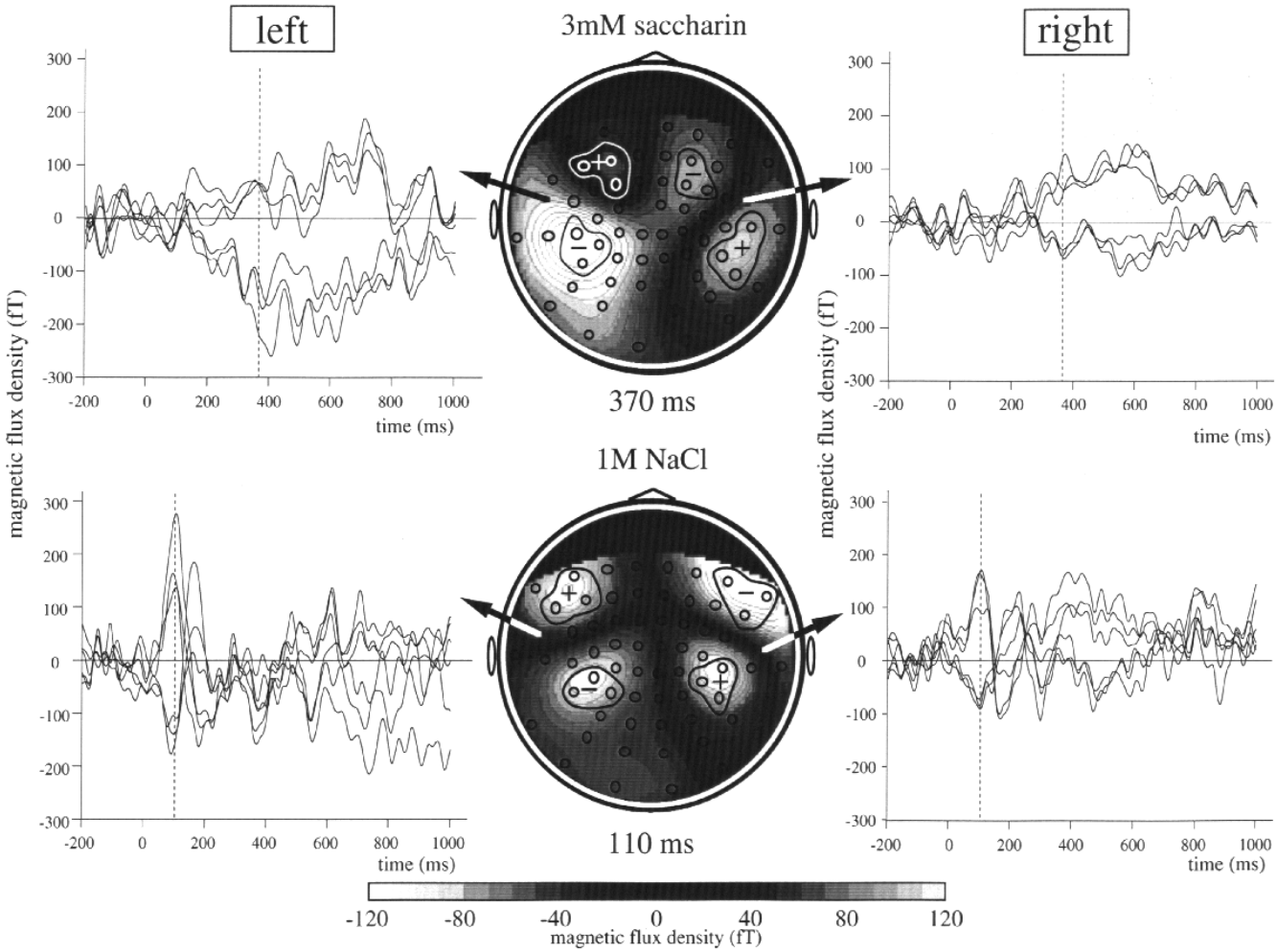

Figure 2 The superimposed magnetic fields of 12 channels out of 64 and isocontour maps over the head, for two tastants. These 12 channels (six channels on each side) had a remarkable response at 370 ms after stimulus onset for saccharin presentation and at 110 ms for NaCl. Both isocontour maps show that the magnetic field was directed from the left-front area of the head to the left-back and from the right-back to the right-front, for both saccharin and NaCl.

Contribution of activation in SI to the first peak of GEMs

In the present study, we detected the first peak of the GEMs regardless of the length of the latency and examined the cortical area which contributed to the production. In each hemisphere of seven subjects in 23 sessions, we chose the single latency of the first change in the GEMs at which we could estimate certain cortical regions clearly, i.e. the time of best fit (TOBF) for the earliest ECDs. In some sessions, two ECDs were estimated in one hemisphere at the first TOBF. Figure 3a,b shows the distributions of such TOBFs in 11 sessions for NaCl and 12 sessions for saccharin respectively.

We found that the total activations were most frequent at75 and 125 ms for NaCl (Figure 3a). Area G was the mostfrequently activated at the first TOBF (12 of the 22 hemispheres examined), followed by the central sulcus (seven hemispheres), the hippocampus (three hemispheres), and the frontal operculum and the parahippocampal gyrus (one hemisphere respectively). Activation of both area G and the central sulcus clearly contributed to the fastest group of the TOBF.

On the other hand, we found that the total activations were most frequent at 225 and 275 ms for saccharin. Area G was the most frequently activated by saccharin (17 of the 24 hemispheres examined), followed by the inferior part of the insular cortex and the hippocampus (three hemispheres respectively), and the frontal operculum and the parieto-occipital sulcus (one hemisphere respectively). No activation in the central sulcus was observed for saccharin sessions. Activation of area G was seen at the shortest latency and no other cortical region was activated at that latency.

The average latency of TOBF for NaCl was 155 ± 45.0 ms, and for saccharin 267 ± 91.7 ms. The difference in latency of the two tastants was 112 ms.

Thus, area G was most frequently activated by two different tastants, NaCl and saccharin, with the shortest

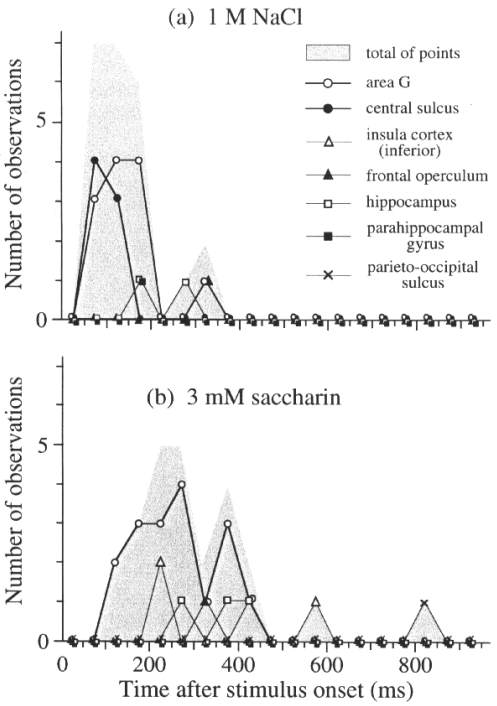

Figure 3 Distribution of the first peak latencies of the GEMs, shown by frequency polygon, in response to two tastants, 1 M NaCl **(a)** and 3 mM saccharin **(b)**. The ECDs were estimated with the best fit in cortical regions at these time points (TOBF), in 11 sessions for NaCl and 12 sessions for saccharin with seven subjects. Different symbols indicate different cortical regions, as shown in the figure. Hatched graphs represent the distribution of the total number of observations at each time point.

latencies. The results confirm our previous finding (Kobayakawa *et al.*, 1996b) that the transition between the insular cortex and the operculum was the primary gustatory area, or area G. The activation of SI was observed only in response to NaCl. This area, therefore, might be related to coding of some aspect of taste for NaCl.

Precise location of area G

Figure 4 illustrates the locations of ECDs in area G, estimated in four sessions (two saccharin on the upper line and two NaCl sessions in the lower) of one subject. Figure 4b shows coronal sections passing through the center of anterior and posterior commissure. Parts A and C of the figure are left and right sagittal sections passing through the neighborhood of the insular cortex respectively.

In each part of the figure, the center of the cross is the average location of the ECDs in the first period when the ECDs were estimated with >80% goodness of fit. The lengths of the bars from the center represent 1 SD in each direction. The length of the each bar is <5 mm in most cases, except in one case for NaCl, in which it is 12 mm, and the estimated ECD moved from the bottom of the central sulcus to area G during this period.

In Figure 4b, the central sulcus (white arrow) is seen abovearea G. Since the central sulcus runs on the lateral surface of the cortex in the dorso-posterior to ventro-anterior direction, the MRI findings indicate that area G is situated posterior to the central sulcus; that is, area G is at the transition between the parietal operculum and the insula in the human. When the anterior end of the lateral sulcus was set as 0 and its posterior end as 100%, the foot of the central sulcus was located at 43.6 ± 6.3% and area G at 80 ± 19% from the anterior end of the lateral sulcus.

Estimation of cortical areas subsequently activated after area G

To examine the cortical areas activated sequentially after the first activation in area G in either hemisphere, we located ECDs by finding the TOBFs at various peak latencies upto1500 ms after the onset of stimulation. We found 176 activated regions in a total of 46 hemispheres and analyzed them. In some sessions, ECDs were repeatedly located in thesame cortical regions of one hemisphere. Among the activated regions, the hippocampus was indicated in 22 time points, the superior temporal sulcus in 23, the parahippocampal gyrus in 19, the frontal operculum in 13 (including the anterior part of the insula in three), the central sulcus in nine, the intraparietal sulcus in eight, the caudate nucleus infour, the inferior part of the insular cortex in four and thecingulate gyrus in four (Figure 5). Activation of all the regions examined was found in both hemispheres. Locations of activations in the central sulcus were just above those inarea G, and clearly lower than those produced by radial nerve stimulation (Yang *et al.*, 1993).

We investigated the latencies of activations in various regions. The average latency of TOBF in area G was 155 ms in response to NaCl and 267 ms in response to saccharin. To utilize all values obtained by NaCl and saccharin and to plot them on the same histogram, the differential latency of the two tastants in activating area G (267 – 155 = 112 ms) was subtracted from the latency for saccharin in each session. The latency distributions of activations of various regions are shown in Figure 6, where the fastest activations (blank bars) are differentiated from the later ones (hatched bars). As indicated in Figure 6b–e, the activities were produced in various regions of the cortex with different latencies after area G. In particular, it was found that the fastest activations of the frontal operculum anterior to area G (in Figure 6b; mean 447 ± 320 ms) started at 286 ms behind those of area G (in Figure 6a; mean 161 ± 77.4 ms). It is also apparent that the activities of the parahippocampal gyrus, the hippocampus and the superior temporal sulcus were delayed, though clear modes were noticeable in the histogram for hippocampus (mode 350 ms, mean 393 ms) and superior temporal sulcus (mode 350 ms, mean 584 ms). The superior temporal sulcus was the last to be activated among the areas observed.

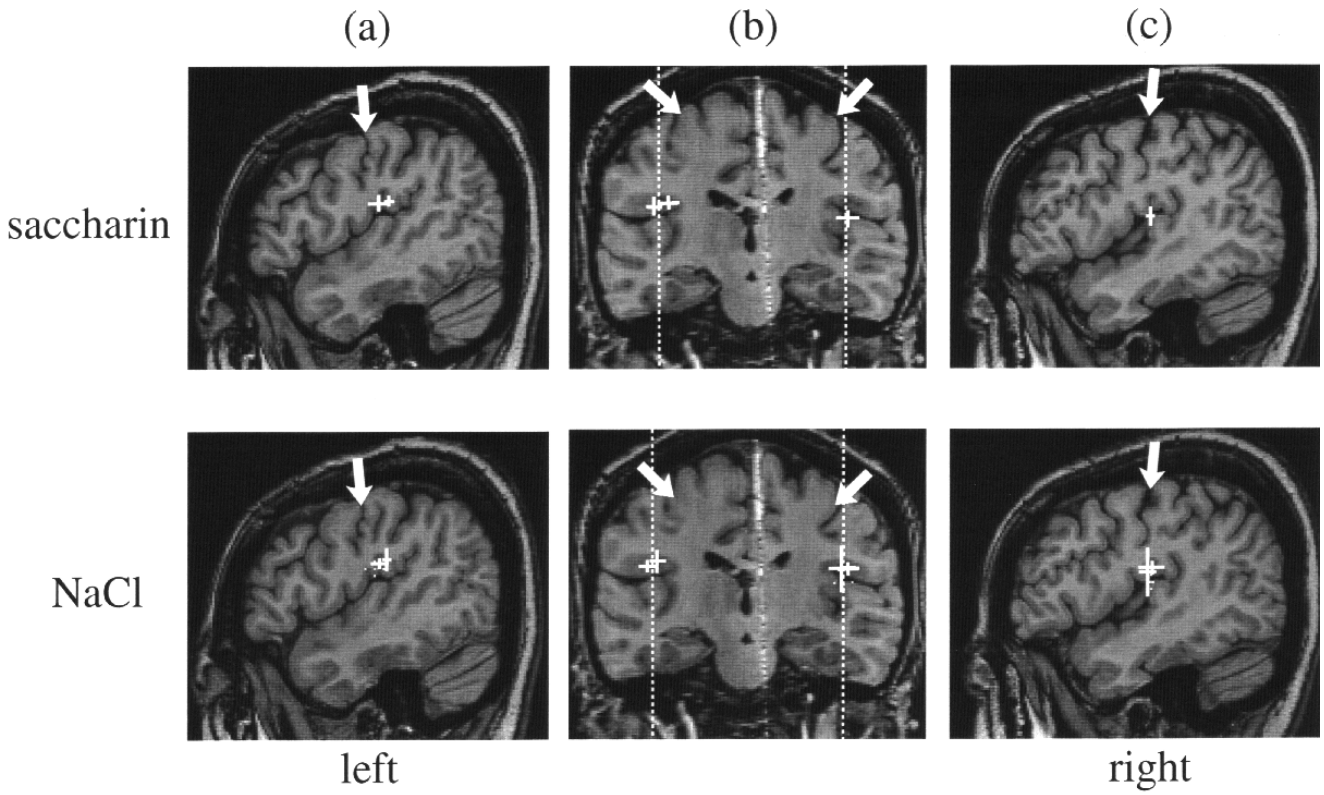

Figure 4 Locations of ECDs in area G plotted on MR images for one subject with four sessions (two NaCl and two saccharin sessions). **(a)** A left sagittal section passing through the neighborhood of the insular cortex; **(b)** a coronal section located 2 cm posterior to the anterior commissure; and **(c)** a right sagittal section passing through the neighborhood of the insular cortex, lateral to section (a). Positions of the sagittal planes (a) and (c) are shown in (b) by dotted vertical lines. The center of the cross is the average location of the ECDs in the first period when the ECDs were estimated with >80% goodness of fit. The length of the bars which are directed to three directions from the center show 1 SD in each direction, in that period. White arrows in all three images show the central sulcus, running from the dorsoposterior to the ventroanterior direction on the lateral surface of the cerebral cortex.

Discussion

Relation between the bottom of the central sulcus (SI) and area G

In response to NaCl, a region in the central sulcus was first activated in seven of the 22 hemispheres, which was less frequent than in area G (n = 12). The region was located at the bottom of the sulcus but not at the postcentral bank. On the other hand, the central sulcus was rarely activated by saccharin. Thus, this region may not be related to both taste stimulations, but only to some aspect of NaCl stimulation. The lower end of the central sulcus was once presumed to bethe primary gustatory cortex (Bornstein, 1940a,b), and ithas been established that thalamic afferents from the parvicellular part of the posterior ventromedial nucleus terminate at both areas G and 3 in squirrel monkeys (Benjamin and Burton, 1968) and macaque monkeys (Ogawa *et al.*, 1985; Pritchard *et al.*, 1986). It is possible that some sort oftaste information is sent to area 3 at the bottom of the central sulcus, and that the latter is activated with taste stimulation as fast as area G. In macaque monkeys, area 3can be activated by electrical stimulation of taste nerves with a latency as short as the activation of area G (Ogawa *et al.*, 1985).

Though we removed the limit of the latency of the first peak of the GEMs, say 200 or 400 ms depending upon taste stimulations, we found area G was the first activated in mostcases. In a few cases, however, short latency activation was not noticeable in area G. This might be attributable to several factors, e.g. a high level of spontaneous activity in the brain which leads to a low signal/noise ratio, a lower level of consciousness such as drowsiness of subjects which blurts activation in area, or changes in the angles between the axes of the SQUID sensors and ECDs. Activation of area 3after a short latency might interfere with that of area G,resulting in difficulty in separation of ECDs in the two neighboring structures. The same argument may be applied to detection of activation in area 3.

Source of difference in the initial peak latency between gustatory evoked magnetic changes to two tastants

The first peak latency of the GEMs for NaCl (155 ms) was much faster than that for saccharin (267 ms), giving a difference of 112 ms. Since the onset latency of potentials evoked by electrical stimulation of chorda tympani is ~9–11

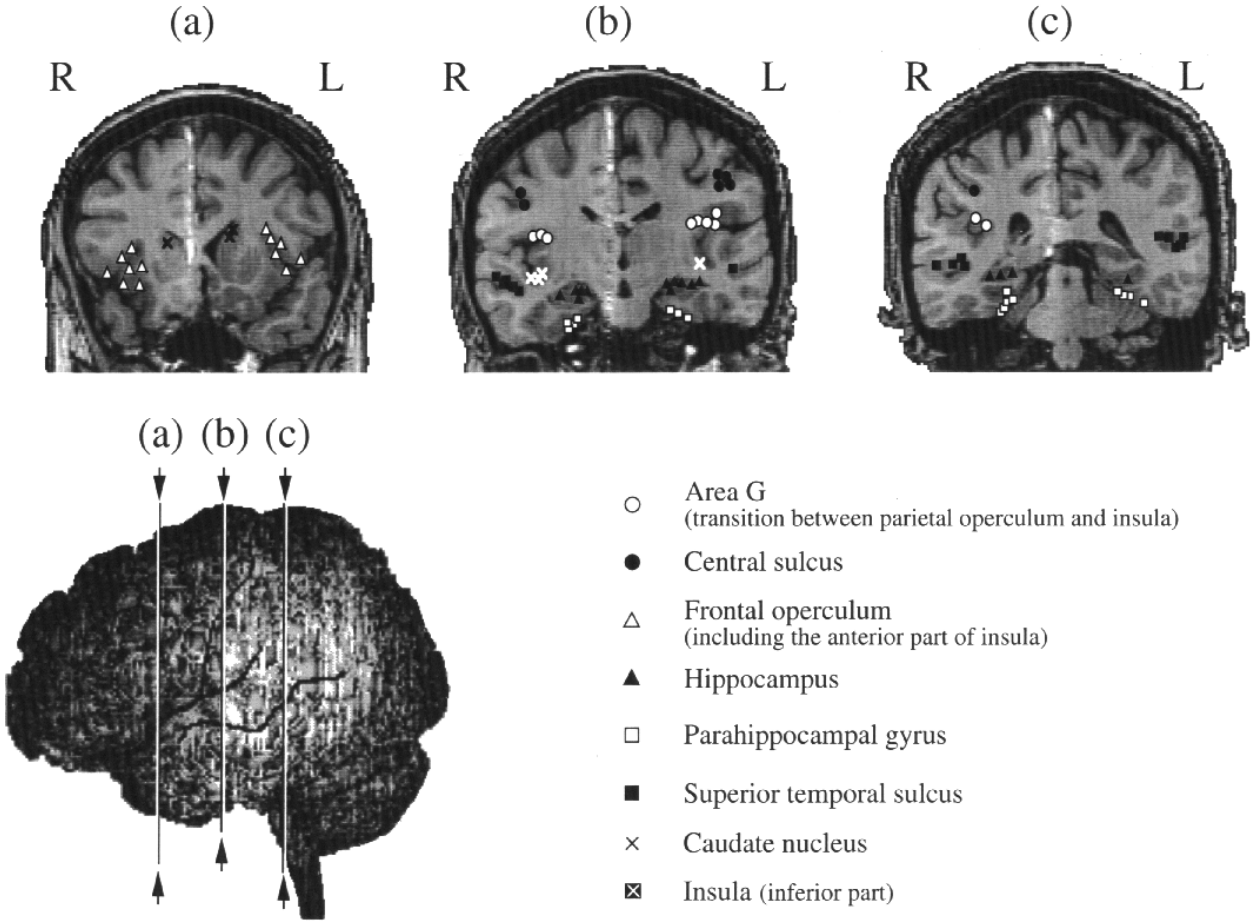

Figure 5 Locations of ECDs in the cerebral cortex and basal ganglia of the seven subjects in 23 sessions. Activation sites in eight regions are plotted at three coronal planes **(a–c)** in the upper part of the figure. Levels of the three planes are shown on the lateral view of the brain in the inset. Different marks indicate activation of different regions, as shown in the figure. R and L represent right and left hemisphere respectively.

ms (Ogawa *et al.*, 1985), most of the latency of GEMs and probably the latency difference between the two tastants may be casued by the receptor mechanism of the receptor cells in the mouth.

Recently it was reported that different receptor mechanisms are involved depending on the tastants at the taste cell membranes (Roper, 1992): sodium activates receptors directly coupled with ionic channels, while sweet substances require intracellular second messengers such as G-protein to open ionic channels. Such differences yield a difference in latency in the generation of receptor potentials at the receptor cells, and ultimately in the onset latency of activation in area G. Our finding that the peak latency for salty taste was shorter than that for the sweet tastant was consistent with the report of Kobal (1985).

Possible differences in the activation of area G between NaCl and saccharin are yet to be studied.

Precise location of the primary gustatory area: whether it is in the frontal or parietal operculum

PET or fMRI studies (Hirsch *et al.*, 1994; Kinomura *et al.*, 1994 ; Small *et al.*, 1997) revealed activation in the frontal operculum and the anterior insula. In addition, some of the investigators presumed the frontal operculum and the anterior insula to be the primary gustatory cortex merely inaccordance with the position of area G in subhuman primates (Ogawa *et al.*, 1985; Pritchard *et al.*, 1986). However, the poor temporal resolution of PET or fMRI makes it difficult to verify this assumption. On the other hand, MEG supplies data with high temporal resolution, allowing identification of the human primary gustatory area activated with the shortest latency. The frontal operculum and anterior insula were activated at a latency of 470 ms on average, longer than that of area G in the present MEG study. Thus it is indicated that the frontal operculum and anterior insula are not the primary gustatory area.

Our conclusion is that the primary gustatory area in human beings is located at the transition between the parietal operculum and the insula, in contrast to that in subhuman primates. In the human being the gustatory cortex has shifted to the parietal cortex along the antero-posterior axis together with the oral representation zone of

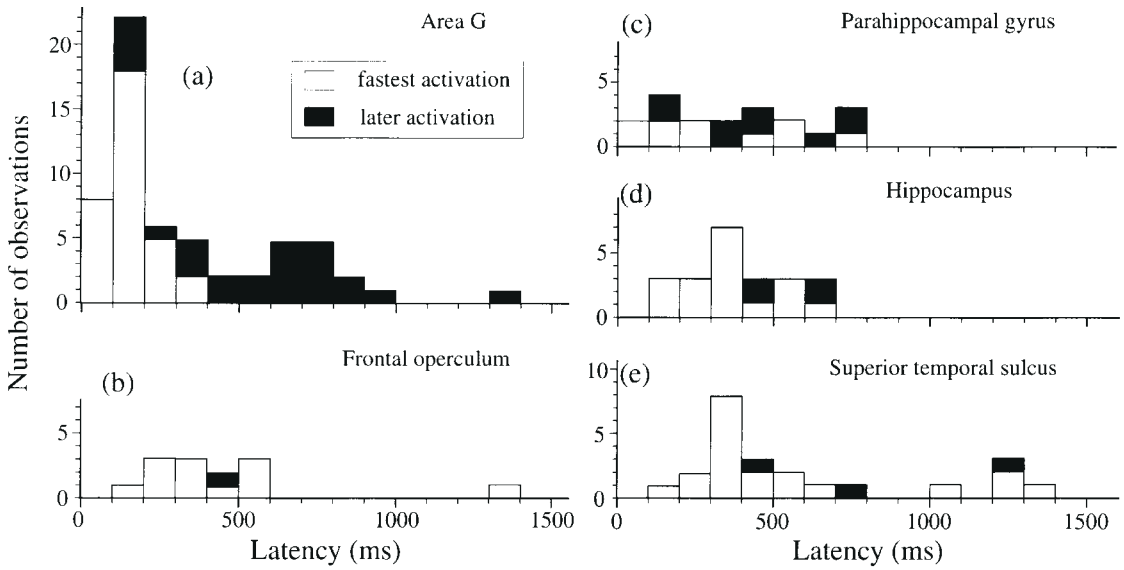

Figure 6 Distributions of latencies of activation in five cortical regions in human GEMs. Blank bars show the shortest latencies in each hemisphere in each session, at the time point at which activation was estimated in the indicated cortical regions, whereas hatched bars show the latencies at which the indicated regions were estimated for the second or third time in the hemisphere in the session. Data was based on both hemispheres in 11 sessions with NaCl stimulation and 12 sessions with saccharin stimulation. The average difference in activation of area G between NaCl and saccharin stimulation (112 ms) was subtracted from the latencies in saccharin sessions to collectively plot data from both stimulation sessions. For **(a)** area G, the average of the shortest latencies was 161 ± 77.4 ms (n = 33) and that of the total was 346 ± 288 ms (n = 59); **(b)** the frontal operculum, 447 ± 320 ms (n = 12), 445 ± 306 ms (n = 13); **(c)** the hippocampal gyrus, 353 ± 232 ms (n = 10), 406 ± 234 ms (n = 19); **(d)** the hippocampus, 359 ± 149 ms (n = 18), 393 ± 158 ms (n = 22); and **(e)** the superior temporal sulcus, 552 ± 366 (n = 20), 584 ± 373 ms (n = 23).

the somatosensory area incomparison with the location insubhuman primates. This is probably because of the enlargement of the frontal association area in the process ofevolution: area G is located near the anterior end of the lateral sulcus in squirrel monkeys (Benjamin and Burton, 1968), moves posteriorly towards the central sulcus but still remains anterior to it in macaques (Ogawa *et al.*, 1985; Pritchard *etal.*, 1986), and moves further backwards traversing the central sulcus to the parietal cortex in human beings. Such movement of sensory areas on the cerebral cortex along with phylogenetic evolution is also known in other areas: the visual cortex is present at the lateral surface of occipital cortex in subhuman primates, but it turns the occipital pole to reside at the mesial surface of occipital cortex in the human brain because of the development of the parietal and temporal association areas.

Table 1 Activated cortical regions detected by MEG, compared with those by PET (Kinomura *et al.*, 1994)

	MEG	PET
Transition between parietal operculum and insula	◎	×
The region including both the frontal operculum and the anterior	○	○
Part of the insula	○	○
Parahippocampal gyrus	○	○
Hippocampus	○	○
Superior temporal gyrus (sulcus)	○	○
Caudate nucleus	△	○
Cingulate gyrus	△	○
Lingual gyrus	×	○
Thalamus	×	○

In the MEG column, the double circle represents the regions most frequently activated (>20% in 176 ECDs), single circles the regions frequently activated (5–20% in 176 ECDs), triangles those rarely activated (<5% of cases in 176 ECDs) and crosses the regions activated in no session. In the PET column, the circles represent the regions activated and a cross the region not activated.

Gustatory related cortical areas other than area G

Table 1 summarizes cortical regions activated by gustatory stimulation in the present study, compared with those observed by PET (Kinomura *et al.*, 1994). Both findings were similar except for the lingual gyrus and thalamus, which were only found with PET. Activation of thalamus probably does not yield magnetic field changes large enough to be detectable by MEG due to its structure.

Since the frontal operculum and the anterior insula were activated at a latency longer than that of area G, they may serve as higher gustatory areas like the precentral opercular area (PrCO) and the orbitofrontal opercular area (OFO) inmacaque monkeys (Ogawa, 1994). Small *et al.* (1997) observed activation in the orbitofrontal cortex by fMRI or PET and suggested it to be a higher gustatory area, as in macaques (Rolls, 1989). In our MEG experiments, however, no ECD was detected in the orbitofrontal cortex. Probably

the ECDs generated from the orbitofrontal cortex lie mainly in the radial direction to the SQUID sensors and escape from detection by MEG.

Activity in the hippocampus and parahippocampus was observed in both PET and MEG studies. However, the spatial accuracy of hippocampal ECD locations is assumed to be poor in MEG because their location in the cranial cavity is as deep as the brainstem, which is not accurately located by MEG. Activity within these structures may be ascribed to the nature of the tasks imposed on the subjects. Subjects in the PET study were asked to discriminate NaCl from water and those in the MEG study had to report on the quality and intensity of taste they perceived.

Kettenmann *et al.* (1996) found magnetic field changes inand around the superior temporal sulcus for olfactory stimulation. Taking into consideration the fact that this is an area associated with various sensory modalities, it is highly possible that the STS is one of the areas associated with both gustatory and olfactory information.

The frequency with which activation in a given area was detected by MEG was dependent upon both the area concerned and the subject examined: area G was activated as the fastest activation site in almost all sessions, with a fewexceptions in which activation in area G was missing or replaced by that in the central sulcus, whereas activation inthe intraparietal sulcus and the frontal operculum was seen in only two subjects. When the activated areas were scrutinized for every subject, it was noticed that activation inthe hippocampus was missing when the superior temporalsulcus or caudate nucleus were activated. It is not clear whether such individual variations in activation sites are due to individual variations in taste coding in the brain or failure of the algorithm to estimate ECDs in the two regions.

In the present study, we found repeated activations of asimilar region, particularly area G and its surroundings, for a long time period, say 1500 ms, after stimulation onset. Such a finding could not be made by PET or fMRI with their poor temporal resolution, though it may indicate that area G and/or some other regions are repeatedly referred to even during a simple gustatory cognitive task as in the present study.

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